



Simulation of shoot chloride accumulation: separation of physical and biochemical processes governing plant salt tolerance

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Received 14 July 1997. Accepted in revised form 29 May 1998

Abstract

Dalton et al. (1996) showed that increasing root temperature from 18 °C to 25 °C increases the root zone salinity threshold value (i.e. a critical value above which yield is reduced) to tomato by 96%. In contrast, the threshold value of a new dynamic salinity stress index, SSI, was found to be invariant to root temperature. This paper shows through model simulation and greenhouse experiment that (1) the apparent increase in salt tolerance is a physical manifestation of the dynamics of salt loading to the shoot and does not reflect fundamental changes in biochemical processes affecting salt tolerance and (2) that the root temperature invariance of the threshold value of the SSI represents an intrinsic property of the plant related to the biochemical mechanisms of salt tolerance, thereby separating the physical and biochemical processes governing plant salt tolerance. These hypotheses are tested in part by simulating shoot chloride accumulation in terms of a temperature dependent physical-mathematical model describing the simultaneous transport of water and salt into the shoot of a transpiring plant and comparing the model output with experimentally determined chloride accumulation in tomato plants (*Lycopersicon esculentum* Mill.) grown in a greenhouse and in nutrient solution at root temperatures of 18 °C and 25 °C and respective root zone chloride concentrations of 33.2 and 63.4 mmol. Root surface area development rates and cumulative water use were measured as input parameters to the model. Experiment and model showed good agreement at 18 and 25 °C. The shoot chloride simulations for two environments with different growth potentials demonstrate that the salt accumulation process is controlled by the transpiration rate, the development rate and biophysical transport properties of the root. Chloride concentration in the root zone is just one of many physical parameters affecting the critical salt accumulation rate, relative to growth, that is necessary to reduce yield.

Introduction

Correlations between yield and root zone salinity have been the basis for most studies on whole plant response in saline environments for many agricultural crops (Maas, 1986). While there are no quantitative models that address the effect of environment on plant salt tolerance, it is generally acknowledged that environment plays an important role (Hoffman and Jobes, 1978). The possibility of physical factors interacting with biochemical or genetic components confound our attempts to provide an adequate definition of 'plant salt tolerance'. While there are numerous studies on

biochemical and genetic factors which may affect plant salt tolerance (Munns and Termaat, 1986) there are no studies that quantitatively relate the effect of physical factors on salt tolerance. Neither is there a clear consensus as to the location, in shoot or root, of biochemical mechanisms affecting salt tolerance (Serrano and Gaxiola, 1994).

Recent hydroponic greenhouse studies of the root temperature dependence of the vegetative yield of tomato showed that an increase in root zone temperature from 18 °C to 25 °C caused a statistically significant increase (96%), in the threshold value of root zone salinity (Dalton et al., 1997). At 18 °C, the threshold value was 33.3 mmol Cl and at 25 °C, the threshold value was 63.4 mmol Cl. These results

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are in agreement with previous qualitative studies by Dalton and Poss (1989) for tomato and by Mozafar and Oertli (1992) for barley. In both of these studies, an optimum root temperature for salt tolerance was observed between temperatures ranging from 10 °C to 30 °C: 25 °C for tomato (6 salinity treatments), and 15–20 °C for barley (three salinity treatments). Neither of these studies had sufficient salinity treatments to quantify statistically the effects of temperature on the threshold value. Moreover, the salinity treatments for barley were below the threshold value of 8 dS/m reported by Maas (1986). While the photon flux for tomato was greater than $1500 \mu\text{mol m}^{-2} \text{sec}^{-1}$, that for barley was only $500 \mu\text{mol m}^{-2} \text{sec}^{-1}$. Recent unpublished data show that reduced photon flux significantly alters the plant response function, at least when based on the osmotic potential of the root zone. Using root zone solution osmotic potential as a correlative index for the activity of biochemical mechanisms related to salt tolerance, can be of limited use in environments with different growth potentials. Similarly, soil water salinity assessment for irrigation management, crop selections and crop modeling based on root zone salinity can be unsuitable when applied in different regions with variable environments.

The concept of a dynamic salinity stress index, SSI, was proposed in an attempt to create a correlative index that (1) gives a useful correlation to plant response in saline environments, (2) takes into account more than root zone salinity and, at the same time, (3) is quantitatively linked to the effects of variable environmental conditions that influence growth potential (Dalton and Poss, 1989; Dalton et al., 1997). The dynamic salinity stress index (SSI) was defined as the total accumulation in the shoot of the dominant salinizing anion (in this case chloride) relative to growth. This index is easily determined by experimental measurement. While the published salt tolerance indices of root zone salinity are a measure of salt concentration *outside* the plant, the dynamic index represents an average salt concentration *inside* the plant without regard to partitioning. In contrast to the large temperature dependence of the root zone salinity threshold values, the threshold values of the dynamic indices were statistically independent of root temperature (Dalton et al., 1997). It will be shown later how this index is quantitatively linked to dynamic processes in the soil-plant-air-continuum (SPAC) that simultaneously affect shoot/root growth and water use.

How is it that such a dramatic shift in apparent plant salt tolerance (root zone salinity criteria) is in-

duced by such a small change in root temperature? Is there a genetic or biochemical salt tolerant mechanism that is root temperature dependent? Or are these changes in root zone salinity threshold values due to physical processes controlling salt load to the shoot. Since the threshold value of the dynamic index was independent of root temperature and is an intrinsic property of the plant shoot, it was concluded that the onset of yield reduction is explained on the basis of the plant being able to maintain its potential growth only when the amount of salt transported to the shoot, relative to growth, is below some critical value, the threshold SSI (Dalton et al., 1997). The observed temperature dependence of the threshold value of root zone salinity was qualitatively explained on the basis that, at the higher root temperature, the temperature induced increase in growth rate was greater than the associated increase in salt accumulation in the shoot thereby decreasing the SSI value. In order for the shoot to reach a critical chloride concentration at the higher root temperature, it is necessary to increase the ion flux to the shoot commensurate with the temperature induced increase in shoot growth. The necessary increase in ion flux is facilitated by a higher salt concentration in the root zone. In this paper, these speculations are rigorously tested by model calculations of shoot chloride accumulation for tomato grown for an extended period of time at two root temperatures, 18 °C and 25 °C, and at two root zone salinities corresponding to their respective threshold values. Simulated values of total chloride accumulation are then compared with those determined experimentally. Finally, comparisons are made between theoretical and experimentally determined dynamic indices for the two temperature treatments.

Theory

Yield is related to whole plant response through functions involving yield components that represent the partitioning of dry matter to the morphological structures that comprise yield. The development of this theory and its application is concerned with the vegetative component of yield.

The Static Index

Ultimately, salt tolerance must be determined by observing whole plant response in saline environments. This is usually done by using a piece-wise linear regression (threshold-slope model) of experimental data

relating yield to root zone salinity (Maas and Hoffman, 1977). Accordingly, yield remains essentially constant with increasing root zone salinity until a critical threshold value is reached. After reaching this threshold value, yield is reduced at a crop specific rate proportional to increases in root zone salinity. Using a linear switching regression technique, Feinerman et al. (1982) have tested the empirical threshold-slope model against other formulations and determined that it is an acceptable function to evaluate salt tolerance. Root zone salinity, *per se*, is a static index because its value, when correlated with yield, is not affected by variations of other parameters in the soil-plant-air continuum that are contributing to growth. As a consequence, indices of plant salt tolerance based on root zone salinity have no intrinsic attributes that can be used to predict the possible effects of other environmental variables on plant salt tolerance, nor can this index be used as selection criterion for salt tolerance in environments having different growth potentials.

The dynamic index

A dynamic salinity stress index (SSI) was created in an attempt to form a correlative index that is analytically linked to the dynamic processes occurring in the soil-plant-air-continuum related to growth, water use, and salt absorption. A dynamic index should have intrinsic properties related to plant function that can respond to variable environmental forces according to laws of physics and chemistry. These requirements will generally be met if the components of such an index consist of mass and/or energy fluxes in the plant. An example of such an index is the Crop Water Stress Index (Jackson et al., 1981). This index is based on leaf temperature which is an easily measured manifestation of the energy balance at the leaf surface. The index has been found to be a good indicator of drought stress. Because its components can be quantitatively expressed in terms of environmental variables such as net radiation, humidity, wind speed and air temperature, the effects that these variables have on the index can be simulated analytically. The goals for creating dynamic salinity stress indices are similar. We use the concepts of systems analysis and attempt to define the state of a natural system (e.g., plant response to salinity) by judiciously choosing a set of measurable parameters that are linked to the response of the system by a set of mathematical rules (Casti, 1989). One simple and natural choice for a measurable variable that meets the criteria and that can be correlated with

plant response is the amount of salt transported to the shoot relative to its growth rate. The mathematical link connecting this parameter to variable environmental conditions is a previously developed theory relating water and ion transport into the shoot in terms of the bio-physical transport properties of the root system. The theoretical aspects are based on the flow of water and salt between two regions (external root water-internal xylem tissue water) effectively separated by a semipermeable membrane (Katchalsky and Curran, 1965). Dalton et al. (1975) and Dalton and Gardner (1978) assumed salt transport between the two regions to be composed of three components: convection, diffusion and metabolic. The resulting osmotic and hydraulic gradients that developed in the xylem tissue and which depended on the rate of water flow, were used in a set of phenomenological equations to describe the coupled transport of water and salt into the xylem tissue of a root system. Fiscus (1975) made a similar development and applied it extensively to experimental work related to water and salt transport into plants. This concept has also been applied by others to various phenomena related to the hydraulic conductivity of plant root systems (Baker et al., 1991; Katou and Taura, 1989; Katou et al., 1987; Moreshet and Huck, 1991; Moreshet et al., 1987; Nobel, 1991; Shalhevet et al. 1976; Taura et al, 1988). The process is transpiration driven and the total chloride accumulation by a plant over its growing period can be calculated from first principles if, in addition to bio-physical transport properties of the root system, cumulative water use and root surface area development rate are known.

The dynamic index has been conceptually defined as the total accumulation in the shoot of the dominant salinizing anion (in this case chloride) relative to plant growth. This definition allows for an interactive relation between rate of salt accumulation in the shoot and its effect on limiting the maximum potential growth rate for any given environment. The analytical definition of the dynamic SSI can be given in integral form or as the sum of discrete terms. In discrete form, the SSI is given in terms of the sum of discrete daily averages as

$$SSI = \frac{\sum_{j_i}^{j_f} A_r(j) J_s(j)}{\sum_{j_i}^{j_f} G(j)} \quad (1)$$

where $A_r(j)$ is an average root surface area for day j , $J_s(j)$ is the average solute flux for day j and $G(j)$ is the daily incremental growth of the plant for day j . The

sums are evaluated from the initial day, j_i , to the final day, j_f .

The direct calculation of J_s and its dependence on osmotic potential of the soil solution, water and ion transport coefficients of the root, root surface area, and, most importantly, transpiration rate, has been demonstrated previously and was shown to account adequately for the observed relationships between water flux, plant pressure potential and temperature dependent metabolic ion transport, (Dalton and Gardner, 1978; Dalton et al., 1975). The quasi steady state solute flux, J_s in Equation (1) is a function of the transpiration flux, J_v ($\text{cm}^3 \text{cm}^{-2} \text{sec}^{-1}$), nutrient solution concentration, C_1 (mol cm^{-3}), and osmotic potential, π_1 (bars), root membrane transport parameters that include the salt reflection coefficient, σ (unitless), the osmotic permeability coefficient, ω ($\text{mole cm}^{-2} \text{sec}^{-1} \text{bar}^{-1}$), and the temperature dependent metabolic ion transport coefficient, k ($\text{mol cm}^{-2} \text{sec}^{-1}$), and is given by

$$J_s = (1 - S)C_1 J_v \quad (2)$$

where the selectivity coefficient, S (unitless), is a water flux, J_v , dependent function.

$$S(J_v) = \frac{\sigma - nRTk(T)/\pi_1 J_v}{1 + nRT\omega(T)/J_v}, \quad (3)$$

where n is the sum of the cation and anion valencies of the salinizing salt, R is the universal gas constant and T is the absolute temperature¹.

The growth term, G , can take on various forms. By expressing growth as a shoot volume, V_s , the dynamic index, SSI_{sv} , represents an integrated average of salt concentration in the shoot, without regard to partitioning, and can be compared to the root zone salinity as its units are also concentration per unit volume. When growth is expressed on a dry weight basis, the dynamic index, SSI_{dw} , represents the concentration of salt relative to shoot biomass. It was pointed out that the SSI_{dw} is also equivalent to the SSI_{sv} relative to tissue bulk density (Dalton et al., 1997). The unstressed values of these various expressions for growth are limited only by genetic and environmental conditions and represent the maximum genetic potential for growth of the species or cultivars.

Initial experimental investigations used growth measurements based on shoot volume. However, concurrent measurements of whole plant tissue density led

to the understanding that the dynamic index based on bio-mass production, SSI_{dw} , exhibited the least root zone temperature dependence of all indices (Dalton et al., 1997). It is used throughout this analysis and is simply designated the SSI.

Mathematical simulation of shoot chloride accumulation

The theoretical simulation of the dynamic index reduces to predicting the total chloride transported to the shoot over the growing period, and expressing it relative to the experimental measure of plant growth. In this analysis, the total shoot chloride, N^* , is estimated by the method of discrete sums, using daily averages of root surface area, $A_r(j)$ and solute flux, $J_s(j)$,

$$N^* = \sum_{j_i}^{j_f} A_r(j) J_s(j), \quad (4)$$

where j is time in days and j_i and j_f are the initial and final days of growth under salinization. Equation (2) gives J_s in terms of the transpiration flux, J_v , a transpiration dependent selectivity coefficient, S , and the concentration of the dominant salinizing anion in the root zone, C_1 .

Transpiration Flux

The transpiration flux, J_v , in Equation (2) is a variable that depends on the rate of water use relative to the available root surface area across which all transport takes place. A daily estimate of the transpiration flux can be obtained from experimentally measured root surface area development rates, $A_r(j)$, and cumulative water use $W(j)$. For the purposes of this analysis it is assumed that the surface area across which water and ion transport take place is the total geometric surface area obtained by volume and root length density measurements. The uptake rates are assumed to be distributed evenly over this surface. The assumption of uniform distribution of water and ion uptake is a necessary simplification and is least problematic for hydroponic experiments. When modeling whole plant water or ion uptake in the soil-plant-air-continuum, such simplifications are necessary and justifiable (Dalton, 1995).

The root surface area (RSA) development rate, $A_r(j)$ and cumulative water use, $W(j)$ are exponential functions of time where j represents the day of growth.

$$A_r(j) = ce^{dj}, \quad (5)$$

¹ This equation was misprinted in Dalton et al. (1997) with the omission of J_v in the numerator.

$$W(j) = ae^{bj}. \quad (6)$$

The parameters c , and d from Equation (5), a and b from Equation (6) characterize the form of the exponential function and are regressed from experimental data. To obtain the average water use rate for day j , a water use rate function $g(j)$ is created such that the water use rate, $g(j)$, times the fraction of a day, t_p , over which transpiration occurs, is equal to the measured water use for day j .

$$g(j)t_p = W(t_{j+1}) - W(t_j), \quad (7)$$

or

$$g(j) = \frac{W(t_{j+1}) - W(t_j)}{t_p}. \quad (8)$$

Making use of the cumulative water use function, Equation (6), $g(j)$ takes the form,

$$g(j) = \frac{ae^{bj}(e^b - 1)}{t_p}. \quad (9)$$

By assuming that most root development occurs at night, similar to that observed for leaf growth (Boyer, 1968), the average daily transpiration flux can be represented as the ratio of the water use rate for day j divided by the cumulative root surface area for the previous day/night cycle, that is, day, $j-1$. The daily average transpiration flux is then given by

$$J_v(j) = \frac{g(j)}{A_r(j-1)}. \quad (10)$$

Substituting for $g(j)$, as given by Equation (9) and for $A_r(j-1)$, as from Equation (5) gives

$$J_v(j) = \frac{ae^{bj}(e^b - 1)}{t_p c e^{d(j-1)}}. \quad (11)$$

Thus, we have a method to estimate the average daily transpiration flux that, while operating over the transpiration period, duplicates the measured amount of water used by each plant.

Shoot chloride accumulation

Let N_j represent the shoot chloride accumulation for Julian day j for a transpiration period, t_p . If the plant is salinized on Julian day j_i and harvested on Julian day j_f , then the total chloride accumulation, N^* , is given by,

$$N^* = \sum_{j=j_i}^{j_f} N_j. \quad (12)$$

The daily total accumulation of chloride, N_j , is given by the product of the root surface area across which transport takes place, $A_r(j-1)$, and the average daily solute flux $J_s(j)$, given by Equation (2),

$$N_j = A_r(j-1)[1 - S]C_1 J_v(j), \quad (13)$$

where J_v is the average daily transpiration flux from Equation (11). The daily chloride accumulation given by Equation (13) is made explicit in terms of $J_v(j)$ by substituting for S from Equation (3). After some simple manipulation of terms and substituting for $A_r(j-1)$ using Equation (5),

$$N_j = cC_1 e^{d(j-1)} \left[\frac{\alpha_1 J_v(j) + \beta_1}{\gamma_1 J_v(j) + \delta_1} \right] J_v(j), \quad (14)$$

where $\alpha_1 = C_1(1 - \sigma)$, $\beta_1 = k + nRT\omega C_1$, $\gamma_1 = C_1$, $\delta_1 = nRT\omega C_1$. The total chloride accumulation over the entire growing period, beginning on day t_i and ending on day t_f , is simply the cumulative sum of the daily absorption and is given by

$$N^* = cC_1 \sum_{j=t_i}^{j=t_f} e^{d(j-1)} \left[\frac{\alpha_1 J_v(j) + \beta_1}{\gamma_1 J_v(j) + \delta_1} \right] J_v(j) \quad (15)$$

where $J_v(j)$ is given by Equation (11). Inspection of the parameters in Equation (15) reveals that the total chloride absorption is seen to be controlled not only by root zone salinity, C_1 , but also by the temperature dependent bio-physical transport properties of the root, the time dependent transpiration flux and the time dependent development of root surface area. These physical properties exert control of the salt load to the plant. These equations show that shoot chloride accumulation is not a unique function of root zone salinity but is linked through the transpiration flux, J_v to all physical variables in the soil-plant-air-continuum. Equation (15) can now be substituted into Equation (1) in order to simulate the various forms of the dynamic indices. Equation (15) is used to simulate the total shoot chloride accumulation for tomato plants grown at two root temperatures and at two root zone salinities corresponding to their respective threshold values for each temperature. Equation (1) is then used to calculate the SSI.

Materials and methods

A hydroponic greenhouse experiment was conducted in Riverside, California, USA during the winter

months of February-March in order to measure the vegetative yield, root surface area development rates, cumulative water use and shoot chloride accumulation for tomato over a 41-day growing period. Fifteen plants were grown at a root temperature of 18 °C and nutrient solution chloride concentration of 33.2 mmol Cl and fifteen plants were grown at a root temperature of 25 °C and chloride concentration of 63.4 mmol Cl. These salinity levels correspond to threshold values of tomato for each temperature treatment (Dalton et al., 1997). To establish the plant population, tomato seeds (cultivar Heinz 1350, *Lycopersicon esculentum*) were sown in vermiculite on day of year (DOY) 34 and prepared as previously described by Dalton et al. (1997). On DOY 49, 50 and 51, root temperature and salinity treatments were imposed.

In order to obtain estimates of root surface area (RSA) development rates, Equation (5), plants were randomly harvested for each root temperature on Julian days 62, 69, 76 and 84. Root surface area was determined by measuring the volume, V , of fresh roots using Archimedes principle (Raskin, 1993). Total root length, l , was obtained by the method of Tennant (1975). Using an average estimate of root radius, r , the root volume, V , is given by, $V = \pi r^2 l$ and therefore $r = (V/\pi l)^{1/2}$. The effective root surface area is given by $RSA = 2\pi r l$. Cumulative water use was measured weekly only for the plants grown to final harvest and for which experimental and simulated values of SSI were to be determined; 7 replications at 18 °C and 7 replications at 25 °C. Water use was determined over various time intervals, depending on the transpiration rate, by noting the amount of water required to bring each plant container to its original solution volume. These results were corrected for evaporation measurements in four control pots whose only water loss was by evaporation. For the final harvest, on DOY 92, leaf water potentials were determined using a pressure bomb apparatus (Soil Moisture Equipment Co., Santa Barbara, California, USA)². The components of the dynamic index, total shoot chloride and shoot growth were measured. Measurements of shoot dry weight and fresh weight were done by standard methods. The total salt load of the dominant salinizing anion to the shoot, in moles, was obtained by measuring shoot chloride in the leaves and stem. Total chloride transport to the shoot was then calculated as the product of chloride concentration on a dry weight

basis and total shoot dry weight. Chloride determinations were made on dilute acetic acid and nitric acid extracts of leaves and stems by coulometric-amperometric titration (Cotlove, 1963). The dynamic salinity stress index was then calculated as the ratio, millimole chloride to: shoot dry weight (mmol Cl⁻/g).

Root bath temperatures were maintained using controller-driven alternate/simultaneous heating and refrigeration systems. Thermocouples were used in conjunction with a micro-logger to monitor air and root bath temperatures. Bath temperatures were controlled to 18.1 ± 0.1 °C, 17.9 ± 0.5 °C, 25.2 ± 0.3 °C and 25.6 ± 4.0 °C. Air temperature averaged 26.6 ± 3.9 °C with night time low of 16.9 °C and daytime high of 39.2 °C.

Model inputs for simulation of shoot chloride accumulation

Equation (15) is the basis for calculating, from first principles, the total shoot chloride accumulation over the growing period. Root transport coefficients are taken from the literature (Dalton and Gardner, 1978; Dalton et al., 1975). Root surface area and water use were determined for the two treatments of root zone salinity and temperature.

Root surface area

The objective of this analysis was to compare experimental and theoretical SSI values at the completion of the vegetative stage of growth for tomato plants at two temperatures and salinities. The simulation model requires estimates of time dependent root development over the growing period. Since these measurements are destructive, an estimate of the time dependent rate of change of RSA was determined from a subset of plants. One plant per treatment, except for DOY 76 with two plants per treatment, was harvested on DOY 62, 69, 76 84 for RSA determination. On the final harvest, DOY 92, seven plants from the 25 °C treatment and six plants from the 18 °C treatment were harvested and in addition to measurements of yield and chloride accumulation, root surface areas were determined. The RSA data were regressed to the exponential functions, Equation (5), using Axum (Axum TriMetrix, 444 NE Ravenna Blvd., Suite 210, Seattle, WA, 1995)². Table 1 gives the regression coefficients c and d , Equation (5), for each treatment and these function were subsequently used in Equation

² Names and products are mentioned for the benefit of the reader and do not imply endorsement or preferential treatment by the USDA.

Table 1. Regression coefficients of root surface area development rate, c and d (Equation (5)) and cumulative water use, a and b , (Equation (6)), for two root temperature and salinity treatments

Root surface area									
25 °C, 63.4 mmol L ⁻¹ Cl					18 °C, 33 mmol L ⁻¹ Cl				
	$c \times 10^{-3}$	d	n^*	r^{2**}		$c \times 10^{-3}$	d	n^*	r^{2**}
	1.779	0.165	11	0.99		0.769	0.174	12	0.97
Cumulative Water Use									
25 °C, 63.4 mmol L ⁻¹ Cl					18 °C, 33.2 mmol L ⁻¹ Cl				
Plant rep.	a	b	r^{2***}	Water use (L)	Plant rep.	a	b	r^{2***}	Water use (L)
1	0.062	0.132	0.98	10.1	1	0.046	0.131	0.96	8.4
2	0.335	0.114	0.99	10.4	2	0.123	0.120	0.94	8.4
3	0.041	0.132	1.0	7.8	3	0.097	0.123	0.93	8.5
4	0.423	0.112	1.0	11.3	4	0.131	0.123	0.97	10.2
5	0.192	0.121	0.98	13.1	5	0.228	0.116	0.98	11.0
6	0.241	0.120	1.0	13.4	6	0.013	0.148	0.97	8.4
					7	1.028	0.105	0.97	13.9

*Number of observations.

** 0.95 confidence level.

*** 0.95 confidence level and 7 observations.

(15) for model simulations of chloride transport to the shoot. Root surface area development rates were almost identical for the two treatments.

Cumulative water use

Cumulative water use was measured at weekly intervals from DOY 55 to DOY 92 for the seven plants in the 25 °C treatment and the six plants in the 18 °C treatment. These same plants were subsequently analyzed for total chloride and growth. The regression coefficients for cumulative water use a and b , Equation (6), are also given in Table 1 along with total water use. These coefficients are also input parameters for Equation (15) and are subsequently used in conjunction with the above root surface area data to obtain the time dependent transpiration flux, J_v , given by Equation (11). The anomalous differences in water use within each treatment could be due to variability in plants or to variable environmental conditions encountered in the greenhouse, such as shading, root temperature or wind velocity around the shoot depending on its proximity to greenhouse cooling fans. Whatever the reason for the variation in water use, the total chloride accumulation will be seen to rank proportionately with total water use.

Root transport parameters

Model temperature dependent input transport parameters for the root system are taken from the literature and include the osmotic permeability coefficient, ω , and metabolic active ion transport, k , (Dalton et al., 1975). The temperature dependent properties of ω are derived from the temperature dependence of the chloride diffusion coefficient. The temperature dependence of the active uptake term, k , is assumed to be that of a first order chemical reaction which approximately doubles with a 10 °C increase in temperature (Dalton and Gardner, 1978). The reflection coefficient, σ , for the root system is the only adjustable fitting parameter for this model.

In summary, the experimentally measured input parameters include the root zone chloride concentration C_1 , and the regression parameters a , b , c and d from Equations (5) and (6). Model inputs for the two temperatures studied are summarized in Table 2. The model output is the total chloride transported to the shoot over the growing period.

Results and discussion

Total shoot chloride was simulated for each treatment using Equation (15) with the appropriate input parameters from Table 2. Results of model predictions

Table 2. Input parameters for simulation model (Equation (15)).

Root temperature, T	25 °C	18 °C
Root zone salinity, C_1 (mol cm ⁻³ Cl)	6.34×10^{-5}	3.32×10^{-5}
Osmotic potential, π_1 (Bars)	1.83	3.17
Metabolic ion transport, k (mol/cm ² /s)	4.0×10^{-12}	2.6×10^{-12}
Osmotic permeability, ω (mol cm ⁻² s ⁻¹ bar ⁻¹)	0.5×10^{-12}	$.418 \times 10^{-12}$
Reflection coefficient, σ (Unitless)	0.988	0.978
Experimental growth period: days	52–92	52–92
Daily transpiration time, t_p (fraction of 24-hour day)	0.42	0.42
Root surface area regression coefficients c, d	Table 1	Table 1
Water use regression coefficients a, b	Table 1	Table 1

Table 3. Theoretical and experimental shoot chloride accumulation with SSI values for two root temperature and salinity treatments

	Root temperature 25 °C, 63.4 mmol L ⁻¹ Cl				Root temperature 18 °C, 33.2 mmol L ⁻¹ Cl			
	Shoot Cl (mmol)		SSI (mmol/g)		Shoot Cl (mmol)		SSI (mmol/g)	
	Theory	Experiment	Theory	Experiment	Theory	Experiment	Theory	Experiment
Replications	6	6	6	6	7	7	7	7
Mean	43.01	42.07	1.49	1.48	29.42	28.22	1.11	1.08
Std. dev.	4.29	4.86	0.21	0.20	5.19	1.95	0.11	0.01
Std. error	1.75	1.98	0.09	0.08	1.96	0.74	0.04	0.04
95% CL	4.50	5.10	0.22	0.21	4.80	1.80	0.11	0.10

are compared with greenhouse experimental measurements in Table 3. At 25 °C, there is good agreement between simulated and experimentally measured shoot chloride when the reflection coefficient is assigned the value of 0.985. This value of the reflection coefficient compares favorably with a previously determined value of 0.975 reported by Dalton et al. (1975) for whole plant root systems. It follows that plants having a root system with a lower reflection coefficient would exhibit the properties of salt sensitive plants while those with a higher reflection coefficient would represent plants that are ‘salt tolerant’. The reflection coefficients usually found in the literature are for membranes of individual cells. Here, the reflection coefficient represents the salt exclusion properties of a group of cells (epidermis, cortex, endodermis and steele) separating the external solution from xylem tissue solution. The experimentally measured mean total chloride accumulation for six replications at 25 °C was 42.77 mmol and the theoretical simulated mean chloride accumulation was 43.01 mmol with no statistical difference at the 0.95 confidence level. For each plant, the total accumulation of shoot chloride ranks with total water use, which is consistent with Equa-

tion (15). Using the same reflection coefficient as used for the 25 °C treatment, the simulated values of total chloride accumulation at 18 °C are less than those determined experimentally. To account for this, it must be assumed that reflection coefficient is reduced at the lower temperature. By introducing a slight temperature dependence which decreases the reflection coefficient by 1%, from 0.985 at 25 °C to 0.975 at 18 °C, the model is in good agreement with experiment. The mean of the experimentally measured total chloride accumulation for seven replications at 18 °C was 28.34 mmol and the theoretical simulated mean chloride accumulation was 29.42 mmol with no statistical difference at the 0.95 confidence level. While there are no studies in the literature on the temperature dependence of the reflection coefficient, σ , for root systems, these results confirm speculation by Dainty et al. (1963) that reducing membrane temperature also reduces the reflection coefficient. This is an important point which requires further investigation.

Simulated and experimental values of the SSI are also shown in Table 3. Since there were no significant differences between the means of the theoretical and experimental SSI=s, the hypothesis that salt loading

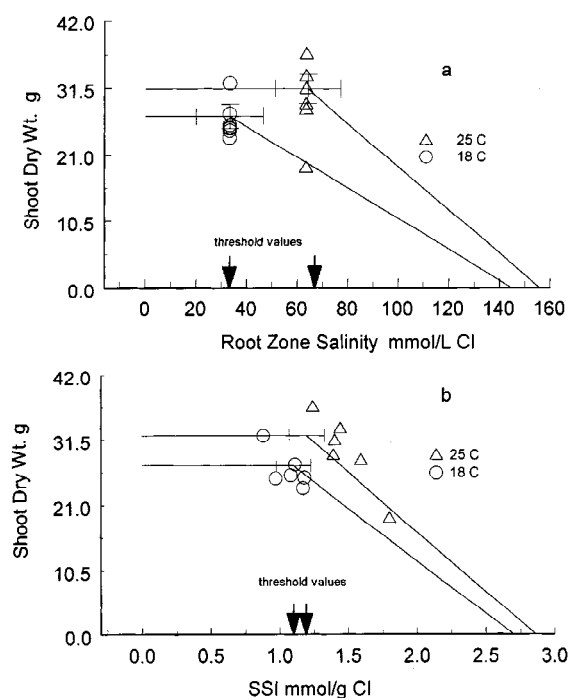


Figure 1. Comparison of yield data (total shoot dry weight) from this experiment with (a) previously determined plant response functions based on root zone salinity and (b) previously determined plant response functions based on the dynamic salinity stress index (Dalton et al., 1997).

to the shoot is controlled by bio-physical root transport parameters for water and salt, and environmental conditions that affect water use and growth is at least partially validated.

Figure 1a shows the yield data from this experiment superimposed on the regressed plant response functions derived from a previous experiment (Dalton et al., 1997). These curves were obtained from parametric regression techniques. The variation of yield within the same treatment, especially for the 25 °C treatment, are normally explained by natural variation within plant populations. Part of this variability can be explained when the same data are plotted in terms of the dynamic salinity stress index, SSI. Figure 1b shows the yield-SSI results from this experiment superimposed on the dynamic plant response function of the previous experiment. It can be seen that the decreasing yield tends towards the higher SSI's, even in the same salinity treatment. There are many factors which can affect chloride accumulation in a population of plants all growing at the same root zone salinity and these are quantitatively expressed in Equation (15). Whatever the cause of variations of growth and wa-

ter use experienced by individual plants growing at a constant root zone salinity, Figure 1b shows that they are following a general pattern of plant response best described in terms of a dynamic index.

It should be noted that root zone chloride concentrations used in this February–March experiment were the threshold value concentrations obtained from the results of an earlier July–August experiment. The growth potential for July–August experiment is greater than for February–March experiment and therefore the chloride concentrations used in the February–March experiment could exceed their respective threshold values, especially for the 25 °C treatment. That is, because of the lower growth potential, the root zone chloride concentration of 63.4 mmol used in this February–March experiment would be expected to exceed the threshold value for this seasonal time period. This would result in SSI values from this experiment yielding slightly larger results than the established threshold SSI, and also would be reflected in smaller yields, all consistent with results shown in Figure 1b.

The mean predawn leaf water potential for the 18 °C treatment was 0.193 ± 0.016 and for the 25 °C treatment was 0.410 ± 0.035 MPa. These results indicate that the plant under the greatest osmotic stress (e.g. lowest root zone osmotic potential and lowest plant leaf water potential) exhibited the largest salt tolerance based on root zone salinity threshold value.

In accordance with this analysis, the highly temperature dependent threshold value of root zone salinity is now understood in terms of the variable root zone chloride concentration necessary to provide the required salt flux into the shoot, according to Equation (15), so that the critical threshold value of the SSI can be reached for the existing environmental conditions governing growth. Root zone salinity is just one component in the SPAC that affects chloride accumulation and therefore cannot be uniquely related to biochemical processes affecting plant salt tolerance in variable environmental conditions. Because physical as well as biochemical processes are acting in parallel, root zone salinity threshold values cannot be used to measure plant salt tolerance under variable climatic conditions that affect water use, growth and salt accumulation.

It is a postulate of this theory, and shown at least for tomato, that as environmental conditions change to lower growth potentials, root zone salinity threshold values will also decrease. In contrast, variations in threshold values of the dynamic index are relatively small, indicating that the fundamental salt sensitive biochemical processes reside in the shoot. Plant

response in saline environments is thus the superposition of two distinct but separable processes: physical and biochemical. Biochemical mechanisms react to a critical chloride level internal to the plant which in turn is controlled by biophysical transport properties of the root and variable climatic conditions affecting transpiration and growth. Root zone salinity is just one of these many parameters.

Conclusions

The accuracy of these simulations give support to the hypothesis that the temperature induced increase (96%) in the threshold value of root zone salinity for tomato is a physical artifact resulting from the dynamic conditions of salt loading to the shoot. And further, the observed increase in the root zone salinity threshold value does not reflect a change in any biochemical mechanisms affecting plant salt tolerance. According to the results of this analysis, the observed increase in threshold value of root zone salinity is the necessary increase in root zone salinity required to increase the solute flux to the shoot relative to the temperature induced increase in growth. The internal salt status of the plant is described experimentally and theoretically by the dynamic index (SSI). It is an intrinsic property of the plant and, especially for variable environmental conditions, is a better correlative index to use for assessing the biochemical and genetic mechanisms affecting plant salt tolerance than is root zone salinity. The results of this analysis show that the magnitude of the dynamic index is primarily controlled by water and salt transport properties of the root system and all variables in the SPAC that affect shoot-root growth and water use. A conclusion with far reaching implications is that yield decline is more fundamentally associated with a threshold value of the dynamic index than it is with the static index of root zone salinity. The experimental work for the validation of these concepts was carried out in controlled greenhouse hydroponic conditions in order that all of the necessary model components could be precisely measured. Working with whole plants growing over an extended period of time, it was shown that salt loading to the shoot could be adequately described by assuming three temperature and transpiration dependent components of salt flux into the root: diffusive, active and convective. With such a validation it can be reasonably assumed that the rate of salt accumulation relative to growth for field conditions will be con-

trolled by the same processes. Simulating an SSI for field conditions requires knowledge of new boundary conditions which are difficult to assess with available instrumentation. However, now a simple experimental field measurement of the SSI can be understood and interpreted in terms of the integrated affects of all the variables in the soil-plant-air continuum that simultaneously affect growth and transpiration. This is vitally important, as it introduces an index which is potentially independent of environment that can be used not only for genetic screening but also for crop modeling, irrigation management, and salinity assessment. The practical importance of these conclusions to diverse areas of research are briefly summarized here.

Irrigation management The quality of irrigation water must be matched with suitable plant response functions for the climate and season of the region. Alternatively, irrigation managers can exploit climatic and seasonal changes in root zone salinity threshold values if they have access to multiple sources of water having different levels of salinity.

Salinity Assessment Because root zone salinity is not the fundamental index for plant response, work in salinity assessment with the objective of predicting crop yield will have to take into account the variability of global environments. There are potential advantages of using the SSI of indicator plants as a method for assessing soil salinity and water use.

Soil water and crop modeling A tacit assumption in all soil-water models that predict yield based on the sum of matric and osmotic potentials of root zone water is that the relation between yield and root zone salinity is fixed for each cultivar or species. While it is thermodynamically correct to add osmotic and matric potential to obtain the total potential, of the soil-water, in general, this cannot be true for the purpose of predicting yield since the osmotic component of stress has been shown not to be the primary causative factor for yield decline. The error in the use of these assumptions for global models will result in the inability to correctly predict yields.

Plant physiology and crop breeding Environmentally induced changes in 'plant salt tolerance' present serious problems for plant breeders. However, the observed changes in threshold values of root zone salinity, according to this analysis, do not necessarily indicate a change in salt tolerance. This work shows that

separate processes, physical and biochemical, operate in parallel and determine the appropriate response for any given environment. One process, salt accumulation in the shoot, is controlled by the physical transport properties of the root and root extent. The second process, a biochemical or physiological mechanism in the shoot, responds to the local internal salt concentration in the shoot. Any experimental determination of plant response to salinity is a manifestation of both of these processes. When research is directed toward genetic or metabolic pathways, it is imperative that the manifestation of these processes on plant response are adequately separated. This work shows, at least for tomato, that salt concentration at the cellular level of the shoot is controlled by biophysical and hydrodynamic processes operating in the root and can be described using Equation (15). Since the threshold value of the SSI appears to be fixed, not only for root temperature, but also for solar radiation (unpublished data), plant screening based on the dynamic index offers a method for unifying plant salt tolerance studies carried out in a myriad of climatic conditions that exist throughout the world.

Comparing nutrient solution osmotic potentials for the two temperature treatments we find that the plants growing at the lowest osmotic potential (greatest stress), by a factor of two, are the plants showing the most vigor. The same comparison holds for leaf water potential. These results are opposite to those predicted when using the general concepts of the effects of osmotic stress on growth, and requires further study.

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Section editor: T J Flowers